Different Effects of Species Diversity on Temporal Stability in Single-Trophic and Multitrophic Communities

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ABSTRACT: The question of how species diversity affects ecological stability has long interested ecologists and yet remains largely unresolved. Historically, attempts to answer this question have been hampered by the presence of multiple potentially confounding stability concepts, confusion over responses at different levels of ecological organization, discrepancy between theoretical predictions, and, particularly, the paucity of empirical studies. Here we used meta-analyses to synthesize results of empirical studies published primarily in the past 2 decades on the relationship between species diversity and temporal stability. We show that the overall effect of increasing diversity was positive for community-level temporal stability but neutral for population-level temporal stability. There were, however, striking differences in the diversity-stability relationship between single- and multitrophic systems, with diversity stabilizing both population and community dynamics in multitrophic but not single-trophic communities. These patterns were broadly equivalent across experimental and observational studies as well as across terrestrial and aquatic studies. We discuss possible mechanisms for population stability to increase with diversity in multitrophic systems and for diversity to influence community-level stability in general. Overall, our results indicate that diversity can affect temporal stability, but the effects may critically depend on trophic complexity.

Keywords: biodiversity, diversity-stability debate, meta-analysis, species diversity, temporal stability, temporal variability.

Introduction

A fundamental property of an ecological community is its stability. Among a host of factors that may potentially influence stability, species diversity has received the most attention. The idea that species diversity may affect stability had its origin at least dating back to Elton (1927), was articulated more explicitly by later investigators in the 1950s (MacArthur 1955; Elton 1958), and was formulated more rigorously via mathematical models in the 1970s (Gardner and Ashby 1970; May 1973; DeAngelis 1975). Despite this long history, it was not until the 1990s that ecologists began to systematically explore the relationship between diversity and stability using observations and experiments. Renewed theoretical interests also surfaced (McCann et al. 1998; Ives et al. 1999, 2000; Yachi and Loreau 1999; Li and Charnov 2001; Ives and Hughes 2002; Thebault and Loreau 2005; Otto et al. 2007). These intensified research activities were largely in response to the increasing awareness among both ecologists and the general public that human activities have caused and will continue to cause tremendous biodiversity loss worldwide (Millennium Ecosystem Assessment 2005). The old academic question thus has metamorphosed into a pressing one: is widespread biodiversity loss causing significant, if any, changes in the stability of the Earth's ecosystems that provide essential products and services for humanity?

Searching for answers to this question has proved to be a nontrivial task, as signified by the long-standing debate among ecologists over the forms of the diversity-stability relationship (MacArthur 1955; Elton 1958; May 1973; Goodman 1975; McNaughton 1977; McCann 2000; Thebault and Loreau 2005). Several factors have contributed to the debate. First, stability can take on a variety of meanings in the ecological literature (Lewontin 1969; Pimm 1984; Grimm and Wissel 1997; McCann 2000; Ives and Carpenter 2007), and different stability properties may show dissimilar, even opposing, relationships with diversity (Pimm 1984; Ives and Carpenter 2007). Confusions arose readily from the indiscriminate mixed use of the term "stability." Second, even for the same stability concept, the diversity-stability relationship may possibly differ between levels of ecological organization (McNaughton 1977; King and Pimm 1983; Tilman 1996). This potential difference, however, was not emphasized during earlier years of the debate. Third, while theories are largely consistent in predicting a positive effect of diversity on community-level stability (Yachi and Loreau 1999; Lehman and Tilman 2000; Ives and Hughes 2002; Thebault and Loreau 2005), their predictions are less consistent on the effect of

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diversity on population-level stability (May 1973; DeAngelis 1975; McCann et al. 1998; Lehman and Tilman 2000; Li and Charnov 2001; Brose et al. 2006). Last and most important, as emphasized by McNaughton (1977), the only approach to resolving the diversity-stability debate is through empirical work. Until relatively recently, however, empirical studies on this topic have been few and sporadic (Pimentel 1961; Hairston et al. 1968; McNaughton 1977).

The accumulation of empirical studies during the past 2 decades offers an excellent opportunity to evaluate whether general relationships exist between diversity and stability. We used meta-analyses to synthesize results of studies that have empirically investigated the effects of species diversity on temporal stability (a measure of the constancy of properties of an ecological system or its components; Grimm and Wissel 1997), arguably the most frequently measured stability property in empirical studies. General patterns (if any) on temporal stability may be relevant for related, less empirically documented metrics of stability, such as resilience. A recent meta-analysis (Balvanera et al. 2006) has examined patterns of relationships between species diversity and a variety of ecosystem properties, including temporal stability; however, the analysis confounded population-level with community-level stability and was based on only a limited number of studies. Here we provided a more comprehensive meta-analysis of existing empirical studies that yielded novel insights into the relationship between diversity and temporal stability at both population and community levels.

Methods

We assembled empirical studies for the meta-analyses by electronically searching the ISI Web of Science database and by manually examining the reference section in the articles identified via the electronic search. Each study included in the meta-analysis met the following criteria: (1) it reported population- and/or community-level temporal stability—or its reciprocal, temporal variability—at multiple levels of species richness; (2) temporal variability (or the reciprocal of temporal stability) was measured using one of two largely equivalent metrics: coefficient of variation of untransformed population- or community-level variables (abundance, biomass, CO_2 production, etc.) or standard deviation of log-transformed variables; (3) simple correlation coefficients between species richness and temporal variability (or the reciprocal of temporal stability) can be obtained. Most studies either directly reported correlation coefficients or presented data or other statistics (e.g., F scores, P values) that allowed correlation coefficients to be calculated (sensu Rosenberg et al. 2000). For a few studies where such information was not directly available, we requested it from the authors. In most cases, correlation coefficients between diversity and population-level temporal stability/variability were reported not for individual species but for individual experiments with all constituent species considered together. Because of this and because data on multiple species from a single experiment/observation are not independent from one another, violating the assumption of meta-analyses, our meta-analyses of the diversity-stability relationship at the population level were based on the experiment-level data (same as the analyses at the community level). We obtained a total of 29 studies (see list of studies in the appendix in the online edition of the *American Naturalist*), which contributed 52 and 21 entries to the community- and population-level analyses, respectively. All these studies reported changes in temporal stability/variability of biomass/abundance in response to changes in species richness, despite our intention to include various types of population- and community-level properties in our analyses.

We classified these studies according to the method of investigation (experimental vs. observational), habitat type (terrestrial vs. aquatic), and trophic complexity (single vs. multitrophic). Experimental studies were those that directly manipulated species richness to examine its effect on stability, and observational studies included those that took advantage of natural diversity gradients or diversity gradients imposed by nutrient manipulations. We defined single-trophic systems as those whose dynamics are not significantly affected by trophic interactions (i.e., those that exhibit single-trophic dynamics). As such, single-trophic systems included algal communities without herbivores, plant communities with little or no influence from major consumers (e.g., large mammal herbivores in grasslands, granivores in arid ecosystems), and communities of bacterivorous protists without their predators. Bacterivorous protist communities generally behave like single-trophic systems in the absence of their predators, with single-species population dynamics well depicted by logistic models and multispecies community dynamics well depicted by Lotka-Volterra competition models (Gause 1934; Vandermeer 1969; Jiang and Morin 2004). Removing studies of bacterivorous protist communities from the meta-analyses did not change our conclusions.

Given that most studies reported temporal variability rather than temporal stability, our meta-analyses were performed on the relationship between diversity and temporal variability, with temporal stability transformed into variability as appropriate. Positive and negative diversity-variability relationships are equivalent to negative and positive diversity-stability relationships, respectively. We conducted the meta-analysis using correlation coefficients between species richness and temporal variability as effect sizes, after undergoing Fisher's z transformation to nor-

malize the data (Rosenthal 1991; Rosenberg et al. 2000). The results of meta-analyses based on different metrics are comparable (Rosenberg et al. 2000), but the use of correlation coefficients allowed us to include a larger number of studies than if other metrics were used, given that different studies may report their data using different statistics and that commonly reported statistics can be readily translated to correlation coefficients. The majority of studies reported correlation coefficients as Pearson's r, with a few as Spearman's ρ; the use of different correlation coefficients, however, should not significantly affect the results of the meta-analyses (Rosenthal 1991).

Mixed-effects models were used to test for the overall relationship between diversity and temporal variability and potential differences in the relationship between experimental and observational studies, between terrestrial and aquatic studies, and between single- and multitrophic studies. Mixed-effects models were also used to evaluate how components of community-level temporal variability—including summed variances, summed covariances, and total community biomass/abundance—changed with diversity; this analysis was based on a subset of studies in our database that have adopted this partitioning practice following Tilman (1999). Mixed-effects models are generally more appropriate for ecological meta-analyses than fixed models that fail to consider the inherent random component of effect size variations (Gurevitch and Hedges 1993). Ninety-five percent confidence intervals around mean effect sizes were generated using 4,999 bootstrap samples and corrected for biases associated with asymmetric distributions of bootstrap values. Mean effect sizes were considered significant if their confidence intervals did not include 0, and mean effect sizes between groups were considered different if their confidence intervals did not overlap. All analyses were performed in MetaWin 2 (Rosenberg et al. 2000).

Results

Meta-analysis across all studies showed that mean effect size at the community level was negative and significantly different from 0 (fig. 1*A*), indicating an overall negative effect of diversity on community-level temporal variability. There were no significant differences in effect sizes between experimental and observational studies or between terrestrial and aquatic studies (fig. 1*A*); this pattern persisted when comparisons were made both within single-trophic studies and within multitrophic studies (fig. 2*A*, 2*B*). Trophic complexity, however, modified the effect of diversity on community-level variability. While mean effect size in single-trophic communities was negative but did not differ from 0, mean effect size in multitrophic communities was significantly negative (fig. 1*A*); confidence intervals for these two groups did not overlap (fig. 1*A*), suggesting overall stronger negative diversity effects on community-level variability in multitrophic than in single-trophic communities. Similar trends were detected when

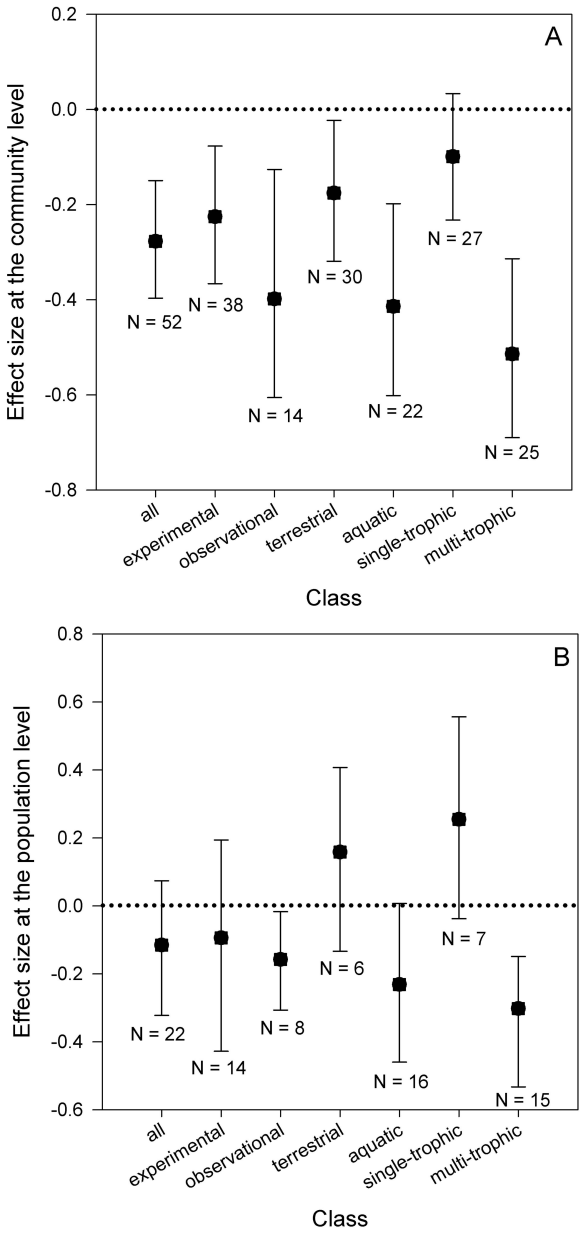

Figure 1: Mean effect sizes (±bias-corrected 95% bootstrap confidence intervals) of the relationship between species richness and temporal variability at the community (*A*) and population (*B*) level. Studies were classified into experimental, observational, terrestrial, aquatic, single trophic, and multitrophic. Effect sizes were Fisher's z transformations of correlation coefficients between species richness and temporal variability. N represents the sample size. The horizontal dotted line indicates the case of effect size = 0.

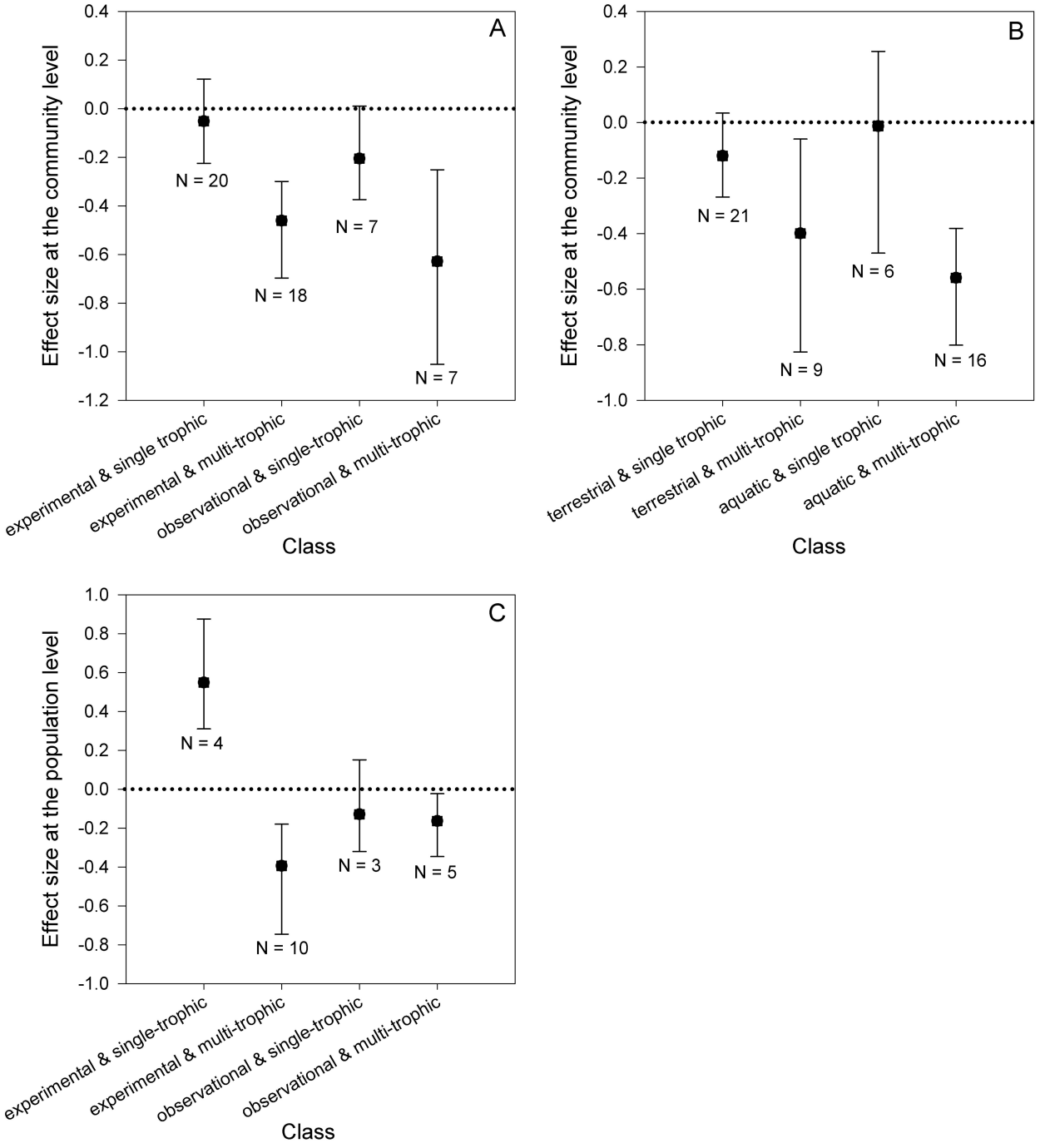

Figure 2: Mean effect sizes (± bias-corrected 95% bootstrap confidence intervals) of the relationship between species richness and temporal variability at the community (*A*, *B*) and population (*C*) levels. In *A* and *C*, Studies were classified into experimental and single trophic, experimental and multitrophic, observational and single trophic, and observational and multitrophic. In *B*, studies were classified into terrestrial and single trophic, terrestrial and multitrophic, aquatic and single trophic, and aquatic and multitrophic. Effect sizes were Fisher's *z* transformations of correlation coefficients between species richness and temporal variability. *N* represents the sample size. The horizontal dotted line indicates the case of effect size = 0.

analyses were done separately for experimental and observational studies (fig. 2*A*) and separately for terrestrial and aquatic studies (fig. 2*B*), although only within experimental studies was mean effect size significantly more negative in multitrophic than in single-trophic communities (fig. 2*A*).

When all studies were considered, the overall mean effect size at the population level was negative but not significantly different from 0 (fig. 1*B*). Mean effect size at the population level was only significantly negative in observational studies and did not differ between experimental and observational studies or between terrestrial and aquatic studies (fig. 1*B*). Within single-trophic systems, mean effect size was significantly positive for experimental studies that differed from mean effect size in observational studies, which was not significantly different from 0 (fig. 2*C*). Within multitrophic systems, however, mean effect sizes were significantly negative and did not differ between experimental and observational studies (fig. 2*C*). Similar to community-level variability, the relationship between population-level variability and diversity depended on trophic complexity. Whereas mean effect size was positive but did not differ from 0 in single-trophic systems, it was significantly negative in multitrophic communities (fig. 1*B*); confidence intervals for the two groups did not overlap (fig. 1*B*), indicating that diversity reduced population-level variability in multitrophic but not single-trophic communities. This difference was largely driven by patterns in experimental studies, where mean effect size was significantly positive in single-trophic communities but significantly negative in multitrophic communities (fig. 2*C*). Within observational studies, single- and multitrophic communities did not differ in their effect sizes (fig. 2*C*). Similar comparisons of terrestrial and aquatic studies could not be performed, because all terrestrial studies included in the population-level analyses were single trophic and all but one aquatic study was multitrophic.

A number of studies included in our analyses have partitioned community-level temporal variability into its various components. Meta-analysis of these studies showed that mean effect sizes for the effects of diversity on both summed variances and summed community biomass/abundance were significantly positive, and mean effect size for the effect of diversity on summed covariances was not significantly different from zero (fig. 3). None of these effect sizes differed between habitat types or between single- and multitrophic systems (data not shown; all but one study were experimental, precluding tests of differences between experimental and observational studies). Analyses performed using only experimental studies produced essentially the same results (data not shown).

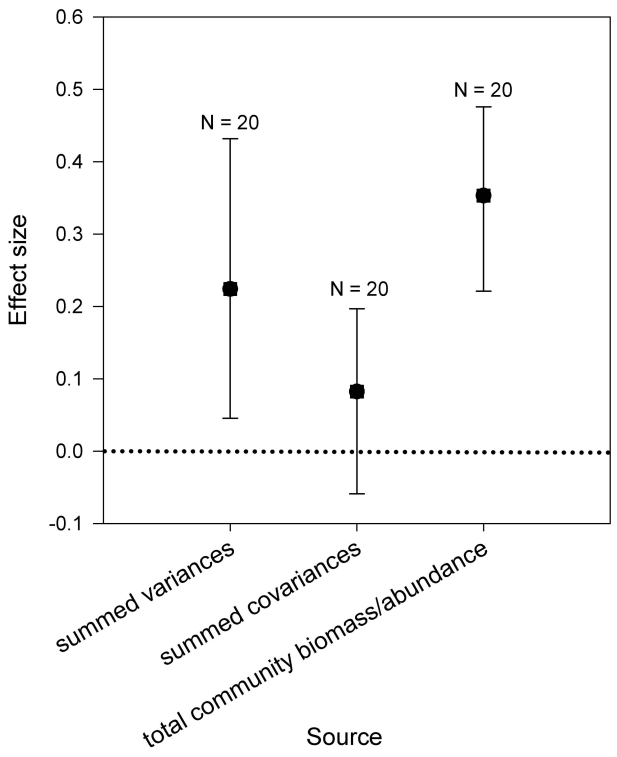

Figure 3: Mean effect sizes (±bias-corrected 95% bootstrap confidence intervals) of the relationship between species richness and summed variances, summed covariances, and total community biomass/abundance. Effect sizes were Fisher's z transformations of correlation coefficients between species richness and the variable of interest. N represents the sample size. The horizontal dotted line indicates the case of effect size = 0.

Discussion

Our analyses clearly show that diversity can affect temporal stability. Community-level temporal stability showed a general trend of increase as diversity increased, driven by the stabilizing diversity effect in multitrophic communities that outweighed the lack of diversity effect in single-trophic communities. Likewise, the effect of diversity on population-level temporal stability was positive in multitrophic communities but nonpositive in single-trophic communities, resulting in the lack of an overall diversity effect at the population level. The relationship between diversity and temporal stability therefore was critically dependent on trophic complexity, with diversity stabilizing population and community dynamics in multitrophic but not single-trophic communities.

It has been suggested that biodiversity decline, which has been most pronounced in the past 50 years of the entire human history and is projected to continue its current trend for at least the near future (Millennium Eco-

system Assessment 2005), may change the magnitude and stability of ecosystem properties (Schulze and Mooney 1993). Direct experimental manipulations of species richness, as the most common approach for examining this idea, have generally found that increasing species richness of a trophic group tends to increase productivity (biomass production) of the group (Cardinale et al. 2006, 2007). Our analyses of the relationship between diversity and community biomass/abundance (fig. 3) add further support to these findings. Observations of natural communities, however, often report other forms of diversity-productivity relationships (Mittelbach et al. 2001). Causes of this apparent discrepancy are still under debate, with some ecologists suggesting that it may be explained by spatial heterogeneity in natural communities confounding the intrinsic positive diversity effect on productivity (Loreau et al. 2001; Schmid 2002) and others attributing it to inherent differences between synthetic communities in diversity manipulation experiments and natural communities (Diaz et al. 2003; Thompson et al. 2005; Jiang et al. 2009*b*). Our analyses, however, indicate that this discrepancy does not seem to exist for temporal stability of community productivity, which exhibited similar responses to changes in diversity in both experimental and observational studies (figs. 1, 2*A*).

The statistical decomposition of community-level temporal variability into three terms (summed variances, summed covariances, and total community biomass/abundance) has prompted a number of studies to investigate how these terms change with diversity, in an effort to uncover the mechanism(s) driving the diversity-stability relationships (e.g., Tilman et al. 2006; Jiang et al. 2009*a*). Increases in community-level stability with diversity may arise in situations where summed variances decline with diversity (the summed variance effect), summed covariances decline with diversity (the summed covariance effect), or total community biomass/abundance increases with diversity (the overyielding effect). Our analyses indicate that the overyielding effect, not the summed variance or covariance effect, was associated with the observed positive diversity-community stability relationship (fig. 3). However, it is important to note that this partitioning approach, as convenient as it is, cannot discern actual mechanisms driving the diversity-community stability relationship. For instance, the significant overyielding effect alone tells little about whether niche complementarity, selection effects, or both (sensu Loreau and Hector 2001) cause community productivity to increase with diversity. Likewise, the nonsignificant summed covariance effect provides little insight on how competitive interactions among species, which are often thought to produce negative summed covariances of species abundances (e.g., Cottingham et al. 2001), change with diversity. Recent theoretical evidence suggests that the sign and magnitude of summed covariances of species abundances in a community depend not only on competition but also on other species and environmental characteristics; as a result, negative summed covariances may be absent even in communities characterized by strong interspecific competition (Loreau and de Mazancourt 2008; Ranta et al. 2008). Further, contrary to the common belief of independent species fluctuations in the absence of species interactions, Loreau and de Mazancourt (2008) showed that species in fact tend to fluctuate synchronously in communities with little or weak competition, leading to the expectation of positive covariances of species abundances in many communities. Empirical observations of natural communities are consistent with this prediction (Houlahan et al. 2007). Therefore, overall there does not seem to be a straightforward relationship between the strength of competition and summed covariances, making it impossible to draw any meaningful conclusions about competition based on summed covariances alone.

Among our most important findings is the differential effect of diversity on temporal stability in single- and multitrophic communities, which was most dramatic within experimental studies that controlled for confounding factors. Theories developed for single-trophic systems generally predict a negative diversity effect on population-level temporal stability (Lehman and Tilman 2000) and a positive diversity effect on community-level temporal stability (Ives et al. 1999; Hughes and Roughgarden 2000; Lehman and Tilman 2000; Ives and Hughes 2002). Our analyses of single-trophic experiments supported the former but not the latter prediction. Theories developed for multitrophic systems also predict a positive relationship between diversity and community-level stability (Ives et al. 2000; Thebault and Loreau 2005) but vary in their predictions on the relationship between diversity and population-level stability (Gardner and Ashby 1970; May 1973; DeAngelis 1975; McCann et al. 1998; Brose et al. 2006). Our analyses, however, show that diversity promoted both population and community stability in multitrophic experiments. Recent experimental evidence indicates that diversity-stability patterns at the population level may strongly influence diversity-stability patterns at the community level (Jiang et al. 2009*a*), especially in the absence of asynchronous/compensatory species responses. We hypothesize that this may have contributed to the congruence between diversity-stability relationships at population and community levels for both single- and multitrophic communities.

Theory emphasizes the importance of the asynchrony of species environmental responses in stabilizing aggregate properties of more diverse communities (Yachi and Loreau 1999; Ives and Hughes 2002; Loreau and de Mazancourt 2008). Unfortunately, summed covariances, which did not

change with diversity in our analysis, do not provide a reliable way to detect the presence and strength of this mechanism. Mathematical rules constrain the lower limits of negative summed covariance values (Brown et al. 2004; Loreau and de Mazancourt 2008), making it difficult to rely on summed covariances to differentiate communities with various degrees of asynchronous fluctuations. Moreover, there is evidence that species in natural communities may oscillate synchronously at one timescale and asynchronously at another timescale (Keitt and Fischer 2006; Vasseur and Gaedke 2007; Downing et al. 2008), likely a result of the operation of different mechanisms at different scales. It is possible that the diversity-stability studies included in our analyses, which generally lasted no more than a few growing seasons or generations of study organisms, may not be able to capture potential asynchrony/compensation among species abundances at longer timescales.

Why would increasing diversity promote population-level temporal stability in multitrophic systems? Current knowledge suggests two possible explanations. First, although randomly assembled food web models predict that diversity tends to destabilize population dynamics (Gardner and Ashby 1970; May 1973), more realistic models incorporating allometric rules suggest that diversity can stabilize population dynamics when predator-prey body size ratios fall into certain ranges (Brose et al. 2006). Empirical predator-prey body size ratios often satisfy conditions for food webs to be stable (Emmerson and Raffaelli 2004; Otto et al. 2007) and for diversity to promote population-level stability (Brose et al. 2006). Second, unlike randomly assembled communities, natural communities are typically characterized by few strong and many weak trophic interactions (Berlow et al. 2004; Wootton and Emmerson 2005). Theory suggests that diverse natural communities may owe their stability to the presence of weak trophic interactions that serve to dampen population oscillations associated with strong trophic interactions (the weak interaction effect; McCann et al. 1998; McCann 2000), an idea supported by a recent experiment (Jiang et al. 2009*a*). Increasing diversity may therefore promote population-level stability in multitrophic communities as the number of weak trophic interactions—hence the importance of the weak interaction effect—increases with diversity (McCann et al. 1998; McCann 2000; Jiang et al. 2009*a*). Note that these two hypotheses are not completely independent, since changes in predator-prey body size ratios are often accompanied by changes in the strength of predator-prey interactions (Emmerson and Raffaelli 2004; Brose et al. 2006).

Two caveats are worth noting. First, despite our initial efforts to include various population- and community-level properties in our analyses, studies that satisfied our selection criteria all examined the stability of biomass/abundance. Further analyses, which require more studies on the stability of non–biomass/abundance properties in relation to diversity, will assess whether our results could be extended to these other properties. Second, sample sizes were uneven across different groups of studies. In particular, most terrestrial studies included only one trophic level (i.e., plants), whereas most aquatic studies had multiple trophic levels. While this may somewhat reflect the inherent difference in the importance of trophic control between terrestrial and aquatic systems (Shurin et al. 2006), small sample sizes in some treatment groups may possibly constrain our conclusions. However, the consistently positive diversity-stability relationships for multitrophic systems and nonpositive relationships for single-trophic systems, observed at both population and community levels, suggest that our results are robust to variations in sample sizes.

In summary, our results support the idea that diversity can affect temporal stability, and they highlight the difference in the diversity–temporal stability relationship between single- and multitrophic communities. This difference underscores the importance of understanding potential stabilizing mechanisms that operate in multitrophic but not single-trophic communities, such as predator-prey body size ratios and the weak interactions effect. To this end, a useful approach is to examine diversity-stability patterns and associated mechanisms for the same empirical systems with and without trophic interactions, which minimizes the impacts of confounding factors that may exist when comparisons are made across different studies. It is notable that few studies have taken this approach (but see Jiang et al. 2009*a*) and that mechanisms underlying contrasting diversity-stability patterns in single- and multitrophic systems remain largely speculative. The same applies to mechanisms contributing to the significant overyielding effect and nonsignificant summed covariance effect found in this study. A challenge but a necessary step for future diversity-stability studies is to move beyond describing patterns to reveal and disentangle mechanisms underlying observed diversity-stability relationships.

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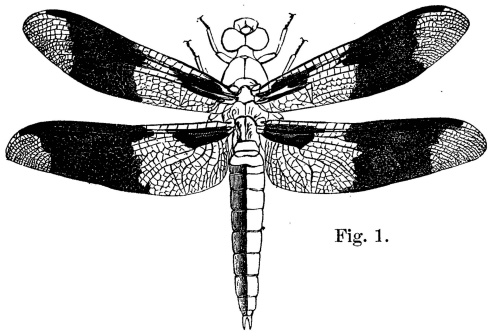

Fig. 1.

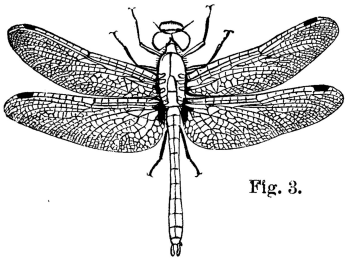

Fig. 3.

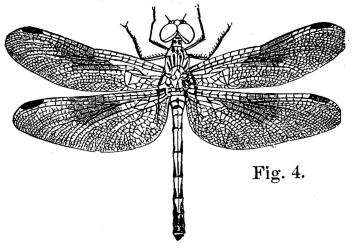

Fig. 4.

The Dragon-fly: "From the moment of its birth until its death, usually a twelve-month, it riots in bloodshed and carnage." 1, the male *Libellula trimaculata* of Count De Geer; 3, male *Diplax berenice* of Drury; 4, female *Diplax berenice*, from "The Dragon-Fly" by A. S. Packard, Jr. (*American Naturalist*, 1867, 1:304–313).